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THE EXTERNAL ANATOMY OF THE PRIMITIVE TANYDERID DIPTERAN MACROCHILE SPECTRUM LOEW, PRESERVED IN BALTIC AMBER.

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Through the kindness of Frau Dr. Richard Klebs, Fraulein Dr. Elizabeth Skwarra, and Professor Dr. K. Andreé, the amber Tipulids of the Klebs Collection, and those of the Koenigsberg Geological Institute, were recently sent to Dr. C. P. Alexander for study; and in this material were practically all of the known specimens of the extremely interesting and primitive Dipteran Macrochile spectrum Loew. Since there were enough specimens of Macrochile for me to be able to make out, in some of them, all of the main features of both sexes, I was delighted to accept Dr. Alexander's suggestion that I make a detailed study of the external features of this interesting and important insect, which has departed but little, in many respects, from the condition characteristic of the ancestral Diptera.

One would have to do considerable "restoring" in attempting to reconstruct the external form of the fossil three- and four-toed horses (such as *Protorohippus*, *Epihippus* and *Mesohippus*) and other extinct Mammalian contemporaries of *Macrochile* in the upper Eocene and lower Oligocene epochs (calculated at between thirty and forty million years ago by Dr. A. C. Lane); but since the hard parts of *Macrochile* are external, and since the imprisoning and preserving gum in which the specimens were imbedded has hardened into a transparent mass, which is beautifully clear in the fine mounts from the above-mentioned collections, it is possible, with a little manipulation, to make out all of the external

details of both sexes, in the long-extinct *Macrochile*—and in examining such well-preserved material, it is indeed difficult to realize that one is not dealing with balsam mounts of recently collected specimens! In spite of the excellent preservation of these insects, however, I do not know of any serious attempt to figure all of the essential external features of both sexes of any fossil insect whatsoever, and on this account it may be of some interest to present the principal external features of both sexes of this primitive Dipteran, which is in many respects one of the most interesting and important representatives of the order thus far known.

As is shown in Figs. 2 and 3, the males of *Macrochile* are holoptic, and the females are dichoptic. Dr. Alexander has called my attention to the fact that hairs occur between the facets of the ommatidia of the compound eyes in all Tanyderids, and he also called my attention to the presence of such hairs between the facets of the eyes of *Macrochile*, thus adding further proof to that from other sources indicating that *Macrochile* is a true Tanyderid—though it is very like the common ancestor of the Psychodids, Tanyderids, and Ptychopterids in some respects. In fact, *Macrochile's* thoracic structures are so annectant between those of the three other families mentioned that I have no hesitancy in grouping the Psychodids, Tanyderids and Ptychopterids in a single superfamily, the Psychodoidea, following a suggestion made by Dr. Edwards (see Crampton, 1926).

As in all other Psychodoids, the ocelli are wanting in Macrochile. The antennae are composed of nineteen segments in both sexes, and are much like those of Tanyderus. In the antenna of the female Macrochile shown in Fig. 13, the postpedicel ppd, or third segment of the antenna, is unusually long, and gives the appearance of being the fusion product of two segments. In the antennae of this female, however, there were nineteen antennal segments as in the antennae of the males, which have a shorter postpedicel (Fig. 14, ppd), so that the abnormally long postpedicel of the female shown in Fig. 13 is apparently not the result of the fusion of two antennal segments. The proportions of the other segments of the antenna do not differ greatly in the two sexes, so that Fig. 13 will serve to illustrate a typical antenna, with the exception of the segment labelled ppd.

The heads of the females shown in Figs. 1 and 3 are somewhat "foreshortened," since I was unable to see the heads properly

(due to the refraction of light when the surfaces of the amber were turned at too great an angle to the source of illumination) when the amber blocks were tilted enough to bring the heads into a horizontal plane, in looking at them from above, so that the mouth-parts are not represented as long as they should be in proportion to the breadth of the head. On the other hand, the base of the proboscis is usually retracted within the mentum bearing the label mn in Fig. 1, in Macrochile, as in other Tanyderids, and in the male Macrochile shown in Fig. 2, the proboscis is unusually extended.

In an article dealing with the labium of the Holometabola (Crampton, 1925), I have given a figure (Fig. 3 of the paper in question) of the labium of Tanyderus, with which the labium of Macrochile here shown (Fig. 1) may be compared. In Macrochile (Fig. 1), the labella lbl, or modified distal segments of the labial palpi, are rather sharply demarked from the basilabella blb, or basal segments of the palpi, in the ventral view of the labium shown in Fig. 1: but in the lateral view of the labium shown in Fig. 2, the basal segments of the palpi are not very clearly demarked, due to the rather poor condition of the specimens showing this aspect of the labium. As may be seen in Figs. 2 and 17, the labella lbl form a trough into which the labrum lr may lie—or its distal portion, at least, is usually overlapped by the labella laterally. The region pgr of the underlip of Macrochile (Fig. 1) represents the united palpigers; and the incomplete suture between the palpigers of Tanyderus has almost completely disappeared in *Macrochile*, in which barely the faintest trace of it can be detected if the lighting is "just right" to bring it out. The elongated sclerite bearing the labels mn and sm in Fig. 1, represents the united mentum and submentum (and is probably largely composed of the mentum) as was pointed out by Crampton, 1925; and in Macrochile this sclerite is somewhat broader, and therefore more primitive, than in the labium of Tanyderus shown in the paper mentioned above. The labium of Macrochile, as a whole, is more primitive than that of Tanyderus, and it is possible that the small area at the bases of the sclerites labelled blb in Fig. 1, represent traces of the missing third, or true basal, segment of the labial palpi; and if this is the case, Macrochile has preserved the rudiments of the basal segments of the labium which are completely lost in every Dipteran I have examined. There were some indications of a thickening and deposit of pigment in the area labelled gu in Fig. 1, which might be interpreted as a tendency to form a gular region in Macrochile.

Due to the fact that there was a great deal of refraction of light when the blocks of amber were tilted at a sharp angle to the rays of light from the lamp used to illuminate the field of the dissecting microscope, I could make out practically nothing of the maxillary structures excepting the maxillary palpi mxp of Figs. I, 2, and 3. The maxillary palpi appear to be composed of five segments, although it is possible that the small basal segment may represent the palpifer. I am more inclined to think that the palpifer is contained in the region at the base of the segment in question, however, so that the maxillary palpi are probably five-segmented.

As is shown in Fig. 17, the labrum lr (which probably represents the so-called labrum-epipharynx) is bent somewhat, so as to lie at a different level from that of the fronto-clypeus fc. The region labelled fc in Figs. 2 and 3, probably represents the united frons and clypeus, and is therefore referred to as the frontoclypeus, although it would perhaps be simpler to call it simply the frons. Behind the region fc in Fig. 3 is a bridge-like area, which is not clearly seen in most specimens. This area separates the frons fc from the parietal region fc usually referred to as the vertex. Posterior to the parietal region fc is the small occiput fc or "nape," which is extremely difficult to make out in the specimens available to me.

On each side of the occiput oc of Fig. 3 is a bulging structure alc (see also alc of Fig. 2) which probably represents the sclerite called the precervicale, or anterior lateral cervical plate, in other Diptera. This area is somewhat larger than in other Tanyderids, and is rather imperfectly chitinized and pigmented. The lateral cervical sclerite lc is somewhat smaller than it is in other Tanyderids (it is extremely elongated in Tanyderus) and I experienced considerable difficulty in making out the outlines of this sclerite in the specimens available to me, so that I am not entirely sure of its exact appearance, although it seemed to have an elongated anterior process (called the cephaliger) extending forward to the occipital condyles of the head. The appearance of the sclerites lc is better shown in Fig. 2 than in Fig. 1, since the parts were considerably distorted in the insect shown in Fig. 1, as is also the case in Fig. 3, in which the neck region is represented as though it were much broader than is the case with more normal specimens.

In Fig. 1 is shown the presternum ps or anterior sclerite of the prosternal region, and a portion of the second sternal plate, or basisternum, is labelled bs in Fig. 1. I could make out practically nothing else of the sternal region of the prothorax in my material, but by combining parts visible in several specimens, it was possible to reconstruct the lateral portions of all of the thoracic segments very satisfactorily, especially since I had been working on this part of the body in lower Diptera recently, and was therefore more familiar with the parts in closely allied forms, and could therefore tell what to look for in Macrochile to better advantage.

I have already discussed the thoracic structures of Macrochile in a paper which will soon be published (Crampton, 1926) dealing with the thoracic structures of the Psychodoidea in general. It will therefore not be necessary to do more than to call attention to some of the more interesting features of Macrochile's thorax, at this time. The pronotum apn and ppn of Macrochile (Fig. 5) is narrower than that of the other Tanyderids I have examined, and in this respect Macrochile is intermediate between the rest of the Tanyderids and the Bruchomyine Psychodids, and it is much nearer the Ptychopterid type than is the case with the pronota of other Tanyderids. The same may be said of the rather elongated coxae and the more elongated (dorso-ventrally) thoracic contour of Macrochile, since in these respects Macrochile is intermediate between the rest of the Tanyderids and the Bruchomyine Psychodids (such as Bruchomyia and Nemoplapus), and it is approached by the thorax of Ptychoptera in this respect. The metanotum mtn of Macrochile (Fig. 5) is likewise intermediate in character between the Tanyderid type and the Psychodid type (exemplified by *Phlebotomus*). As is shown in Fig. 15, the metanotum mtn becomes narrowed mesally, as does that of the Psychodid Phlebotomus, while the lateral portions remain somewhat "oval" as in Phlebotomus.

In *Macrochile*, as in all other representatives of the superfamily Psychodoidea, the meron of the mesothoracic coxa unites with the lower portion of the mesothoracic epimeron to form the area *mpl*, of Fig. 5; and the suture *a* is incomplete as in all Psychodoides. As in all members of the Psychodoidea, there is a rather clearly demarked area *saf* in Fig. 5 of *Macrochile*. The well-known "V-shaped" suture familiar to all students of the Tipulids is incomplete in *Macrochile* (i.e., the suture labelled *s* in Fig. 5), and the metathoracic spiracle *sp* is very near the base of the halter in *Macrochile*, as in all of the Psychodoidea.

The relative lengths of the various segments of the legs are shown fairly accurately in Figs. 19 and 20, and there is nothing strikingly different in them from the structures to be found in *Tanyderus* and similar forms. It may be noted in passing, that there are two movable spines at the apex of the hind tibiae (Figs. 18 and 19); and the pulvilli, empodium, and other structures of this nature are undeveloped, as in most lower Diptera. The claws *un* of Fig. 16 are rather interesting, but do not differ markedly from those of *Tanyderus*.

Of the other thoracic appendages there remain to be considered only the wings and halteres. The venation, as is shown in Fig. 11, is of an extremely primitive type, and the character of the median veins would indicate that the view of Dr. Tillyard as to the four-branched character of media is the correct one. I have therefore adopted Dr. Tillyard's interpretation of the primitive Dipterous venation in homologizing the veins of Macrochile shown in Fig. 11, with the exception of the vein labelled pa, which Tillyard considers as the second branch of Cu in related insects, but which appears to be an intermediate vein, the preanal, regarded by some investigators as the first anal, by others as the second branch of Cu. I prefer to refer to it simply as the preanal vein, since its true relations to the other veins have not been definitely determined. I could not detect any connection between the base of this preanal vein and the cubital or anal veins, in Macrochile, but in Tanyderus forcipatus the base of the preanal vein seems to dip down to the first anal, although the vein is so faint in this region that I cannot be sure in the matter. The anal veins behind the large first anal were greatly reduced, and were very difficult to make out, but they seem to be of the general character of the veins behind the first anal in Tanyderus, so far as I can make them out. The longitudinal veins bear numerous macrotrichiae, but it would obscure the course of the veins to attempt to indicate the occurrence of the macrotrichiae, so that they have been omitted in the figure. I noted macrotrichiae on the membrane of the wing in several instances, but apparently these were detached macrotrichiae which chanced to come to rest upon the wing membrane before the gum hardened into amber.

Dr. Alexander has called to my attention the fact that the cross vein m (Fig. 11) is present in all Tanyderids, and that Macrochile is clearly an "out and out" Tanyderid on this account, although I was inclined to consider Macrochile as rather near the

Psychodid Bruchomyia because of the great similarity between the two in certain thoracic features, which, however, were not sufficiently important to outweigh the evident similarities between Macrochile and Tanyderus in the nature of the head, mouthparts. and other features.

In their general venational characters, Bruchomyia and the Tanyderids have so much in common, that Dr. Alexander formerly included Bruchomyia in the family Tanyderidae—although, of course, later studies have shown that Bruchomvia is a Psychodid. Dr. Alexander's grouping, however, apparently gave the hint to Dr. Edwards who suggested (in litteris) that the Psychodids (including Bruchomyia), Tanyderids and Ptychopterids should be included in a single superfamily; and as soon as I began the study of Macrochile (Crampton, 1926) the synthetic character of its thoracic sclerites at once convinced me that the Psychodids, Tanyderids and Ptychopterids intergrade and should be united in a common superfamily, the Psychodoidea. The venational evidence supports that of the thoracic sclerites, so that all of the structures thus far studied clearly indicate that the three families mentioned should be grouped in a single superfamily.

There are a few peculiar features in the venation of Macrochile which are difficult to interpret. Thus, the stub of a vein at the anterior end of the cross vein r-m is a very puzzling feature which is also present in specimens of Bruchomyia, Tanyderus, and Protoplasa, so that it may have some phylogenetic significance. A fold-like line in this region may indicate the beginning of the formation of the structure which develops into the socalled spurious vein in Syrphidae, and this matter would repay further investigation along these lines.

The stub of a vein projecting beyond (distally) the forking of Sc is another puzzling feature which I do not understand. It was present in one specimen of Macrochile but was absent in all of the other specimens examined. This stub may possibly represent the true first branch of Sc, and in that case, the vein I have labelled Sc_1 in Fig. 11 would be merely a cross vein. This suggestion is offered for what it is worth, since I have not been able to investigate the subject further.

The halter (Fig. 12) presents no features of especial interest, although the nature and location of the projection labelled p in Fig. 5 suggests that this structure may be the precursor of the so-called prehaltere or spatulate appendage in front of the base

of the halter in Ptychopterids.

There are no features in the basal region of the abdomen requiring especial mention, save the fact that in the specimen shown in Fig. 15, the abdomen was bent sharply downward, exposing a rather large intersegmental membrane or conjunctiva *cnj*, which is of somewhat greater extent than in most Tanyderids.

The terminal structures are the most important parts of the abdomen, since these offer characters of specific value, and fortunately, it was possible to make out practically all of the structural details of both sexes in the material available to me. I have therefore given figures of the dorsal, lateral and ventral aspects of the male and female.

The eighth abdominal segment of the female (Figs. 6, 8, and 9) is not greatly reduced as is the case with the eighth segment of the male (Figs. 4, 7, and 10), and the eighth sternite of the female bears a pair of projections labelled vv in Figs. 8 and 9. From their position, one might infer that these projections represent the ventral valves of the ovipositor of lower Holometabola, but I am more inclined to consider them as the homologues of the valvular processes of the hypogynium, or subgenital plate of the female in other insects. I was unable to find similar structures in the females of Tanyderus or Protoplasa, and it is possible that Macrochile is the only Tanyderid in which they occur.

Another peculiar structure occurring in *Macrochile* is the structure labelled *mg* in Figs. 8 and 9. It would be interesting to trace the origin of this structure in order to determine if it has any relation to the dorsal valves of the ovipositor in lower Holometabola, although I doubt that any such relation exists, and it is more probable that the structure in question is merely an out-

growth of the sternal region.

The basal segments of the cerci labelled bc in Figs. 6, 9, and 8 are peculiar in shape, and bear rather sharply pointed ventral processes projecting posteriorly. If the structures labelled bc are not the basal segments of the cerci, they probably represent the paraprocts or parapodial plates, which are in reality modified basal segments of the cerci, although they are not usually recognized as such. If the structures labelled bc are the parapodial plates, the structures labelled dc are the cerci, instead of representing merely the distal segments of the cerci, as the labelling would indicate.

The precerci, or sclerites bearing the label cg in Figs. 6 and 8, possibly represent the tenth, or the united tenth and eleventh seg-

ments, but the homologies of the parts are not clear, and there is evidently considerable need of a thorough study of the terminal structures of both sexes of the Pterygota in general, beginning with the Orthopteroid forms, and including all of the higher types of insects as well.

The ninth tergite epa of the male (Figs. 7 and 10) is much larger than the ninth tergite of the female (Figs. 6 and 8), and the cerci of the male are apparently composed of but one segment, so that the structure labelled bc in Fig. 10 apparently corresponds to the structure labelled bc, alone, in Fig. 8. The anusbearing structure pg is more easily seen in the male (Figs. 7 and 10) than in the female. It probably represents the eleventh segment, although this has not been definitely determined.

The gonostyli or stylus-like claspers of the male insects are usually composed of two segments in the Holometabola related to the Diptera. In the males of *Macrochile*, the basal segments or basistyles *bst* of Figs. 4 and 7 unite basally, or fuse with the neighboring parts as shown in Fig. 4. The dististyles or distal segments of the claspers labelled *ds* in Figs. 4 and 7 bear median projections and outgrowths which are of considerable interest.

As is shown in Figs. 4 and 7, the dististyles ds are forked, and the basal process sap probably represents the precursor of the basal or inner appendage of the dististyle in other Diptera, while the distal process ap probably represents the outer or apical appendage of the divided dististyle of other Diptera. The forking of the dististyle in Macrochile, therefore, probably foreshadows the division of the dististyle into an inner and outer appendage in other Diptera. Between the forks of the dististyle is a projection iap (Figs. 4 and 7) which is small and difficult to see clearly.

Since Macrochile is such a primitive Dipteran in many respects, I had hoped that the condition of the genital styles in it might give some hint of the nature of the genital styles in Diptera in general, but these structures are too highly modified even in Macrochile to be of much use in this respect. It is possible that the genital styles of the Holometabola related to the Diptera may not be homologous with the styli of Orthopteroid males, but the genital styles of these Holometabola may still be called gonostyli, since they are style-like appendages of the genitalia, and the true styli of male Orthopteroid insects might be differentiated from these by calling them androstyli, or simply styli.

The aedeagus aed of Macrochile (Figs. 4 and 10) appears to

be bifid, or it is composed of two parts. Paired projections labelled gap in Figs. 10 and 7, flank a central structure which is very difficult to make out because the amber in this region is very much clouded (due to the inclosure of moisture, etc.) in all of the specimens examined. The structures labelled gap in Figs. 7 and 10, are provisionally termed the "gonapophyses," although this designation is not as appropriate as certain other terms ap-

plied to similar structures.

From the foregoing discussion, it is quite apparent that a detailed study of the external morphology of insects preserved in amber can be made with considerable accuracy and ease, and it is to be hoped that more of the amber insects will be figured in detail, so that their principal anatomical features may be made available for comparison with the structures of living forms, since the amber insects are in many instances more primitive than recent insects; and when they represent synthetic types, as is the case with Macrochile, the study of their anatomy is of the greatest interest and importance from the standpoint of phylogeny.

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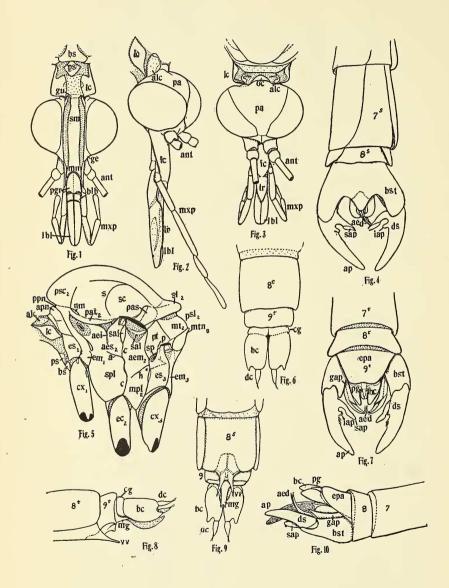
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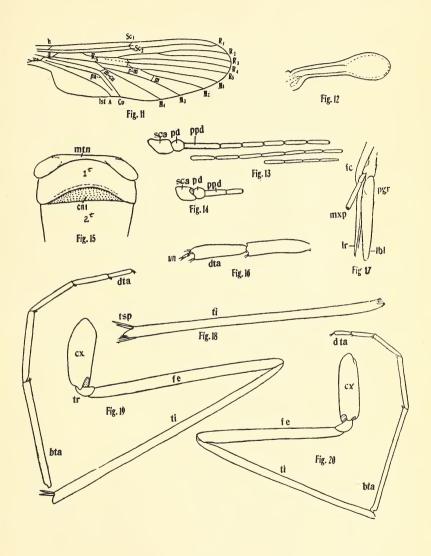
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Abbreviations.

Α	Anal vein.	aei	Anepisternal incision or
a	Arculus in wing veins.		cleft.
a	Anepisternal suture in	aem	Anepimerum or ptero-
	thorax.		pleurum.
aed.	Aedeagus.	aes	Anepisternum.

alc	Precervicale.	mxp	Maxillary palpus.
ant	Antenna.	nm	Notomacula.
ар	Apical or outer process.	oc	Occiput.
apn '	Antepronotum.	р	Prehaltere.
b	Anepimeral suture.	pa	Parietal region or ver-
bc	Basicercus (paraproct?).	-	tex of head.
blb	Basilabella.	pa	Preanal vein of wing
bs	Basisternum of pro-	•	(Cu ₂ according to Till-
	thorax.		yard, 1st A of Com-
bst	Basistyle.		stock).
bta	Basitarsus ("metatar-	pas	Parascutellum or axilla.
	sus ").	pat	Paratergite.
С	Pleural suture.	pd	Pedicel.
cg	Precercus.	pg	Proctiger.
cnj	Conjunctiva.	pgr	Palpiger.
Cu	Cubitus.	ppd	Postpedicel.
cx	Coxa.	ppn	Postpronotum.
dc	Disticercus.	ps	Presternum of pro-
ds	Dististyle.	-	thorax.
dta	Distitarsus.	psc	Prescutum.
ec	Eucoxa.	psl	Postscutellum.
em	Epimerum.	pt	Postalare or Pleuroter-
ера	Epandrium (9th tergite		gite.
	of male).	R	Radius.
es	Episternum.	R_s	Radial sector.
fc	Frontoclypeus.	r-m	Radio-medial cross-vein.
fe	Femur.	s	Scutal suture.
gap	Gonapophysis.	\mathbf{saf}	Subalifer.
ge	Gena.	sal	Subalare.
gu	Gula.	sap	Basal process of disti-
h	Humeral cross-vein.	1	style.
iap	Intermediate process.	Sc	Subcosta.
lc	Laterocervicale.	sc	Scutum.
lbl	Labellum.	sca	Scape.
lr	Labrum or labrum-epi-	sl	Scutellum.
	pharynx.	sm	Submentum.
M	Media.		Spiracle (metathoracic).
m	Median (intermedian)	sp sp1	
	cross-vein.	spl	Sternopleurum. Tarsus.
m-cu	Medio-cubital cross-vein.	ta +:	
mg	Mediogynium.	ti +	Tibia.
mn	Mentum.	tr	Trochanter.
mpl	Meropleurum.	tsp	Tibial spurs.
mt	Mediotergite.	un	Claws or ungues.
mtn	Metanotum.	vv	Hypogynial valves.





EXPLANATION OF PLATES.

- Fig. 1. Ventral view of head of female (slightly tilted upward).
- Fig. 2. Lateral view of head of male viewed somewhat obliquely.
- Fig. 3. Dorsal view of head of female (tilted downward).
- Fig. 4. Ventral view of terminal abdominal structures of male.

Fig. 5. Lateral view of thorax.

- Fig. 6. Dorsal view of terminal abdominal structures of female.
- Fig. 7. Dorsal view of terminal abdominal structures of male.
- Fig. 8. Lateral view of terminal abdominal structures of female.
- Fig. 9. Ventral view of terminal abdominal structures of female. Fig. 10. Lateral view of terminal abdominal structures of male.
- Fig. 11. Dorsal view of right wing.
- Fig. 12. Dorsal view of right halter.
- Fig. 13. Ventral view of right antenna of female.
- Fig. 14. Basal segments of male antenna viewed obliquely dorsally.
- Fig. 15. Dorsal view of metanotum and first tergite.
- Fig. 16. Lateral view of tip of left tarsus of male.
- Fig. 17. Lateral view of terminal portion of trophi of male.
- Fig. 18. Lateral view of right hind tibia of male.
- Fig. 19. Lateral view of hind leg.
- Fig. 20. Lateral view of left fore leg of male.
- N. B.—The subscripts 1, 2, and 3 indicate that the part in question belongs to the pro-, meso-, or meta-thorax. The letter t written to the right and above a numeral indicates the tergite of the segment indicated by the numeral. The letter s indicates the corresponding sternite.

A Correction.—In his paper "Studies of North American Aegeriidae, No. 3," Bulletin, vol. XX, no. 4, p. 157, the author omitted to state the locality for the Holotype of Alcathoe pepsioides. It is Durango, Colo. The spelling of the specific name of the food-plant, "Clematis ligustrifolia," also should be corrected to read "ligusticifolia." Dr. T. D. A. Cockerell has been good enough to call attention to this omission and error.—Geo. P. Engelhardt, Brooklyn Museum.